Dwight (Thos.) Jr.

Dr. Woodward.
With the compliments
of the
Writer.

THE

STRUCTURE AND ACTION

OF

STRIATED MUSCULAR FIBRE.

By THOMAS DWIGHT, Jr., M.D.,

PROFESSOR OF ANATOMY AT THE MEDICAL SCHOOL OF MAINE.

THE

STRUCTURE AND ACTION

OF

STRIATED MUSCULAR FIBRE.

By THOMAS DWIGHT, Jr., M.D.,

PROFESSOR OF ANATOMY AT THE MEDICAL SCHOOL OF MAINE.

[From the Proceedings of the Boston Society of Natural History, Vol. XVI, November 5th, 1873.]

STRUCTURE AND ACTION OF STRIATED MUSCULAR FIBRE.

BY THOMAS DWIGHT, JR., M.D.

It would be alike tedious and superfluous to attempt to recapitulate the various views held on this subject, not only because this has been repeatedly done, but also because most of the methods employed have been so unsatisfactory as to throw doubt on the conclusions.

Fibres have been used after removal from the body, teased out by needles, or flattened by the covering glass, and further affected by the abnormal media (among which even air is to be reckoned) in which they were examined. The contractions occurring under these circumstances are irregular, and mostly short-lived. Another very important objection appears to have escaped attention, namely: that when a muscular fibre is removed from the body it has lost its attachments, and owing to its properties of tonicity and elasticity it must, either at rest or in action, be in different relations from those of the living fibre. Merkel[1] states frankly that he never has been able to follow the steps of contraction. He could see the fibre begin to move, the movement become quicker, and then the contraction would be complete without his having been able to see the intermediate phenomena. He contrived to obtain permanent views of more or less contracted fibres by throwing small parts of living animals into absolute alcohol, which struck the fibres dead in all the stages of vital action, but he has disregarded the chances of error from the specific action of the reagent on the substance of the fibres,

[1] Archiv für Mikroskopische Anatomie, Band VIII, Heft 2.

and on their last movements. Wagener and Engelmann appear to have made some observations on living animals, or on parts of them, but I have seen no detailed account of these studies, and cannot think that they carried them far, for had they done so they certainly would not have relinquished them.

After studying fibres pulled from the legs of flies and grasshoppers, I turned my attention to water beetles, and accidentally discovered that the legs of several of the smaller kinds were sufficiently transparent to give a good view of the muscles *in situ*, but that the genus *Gyrinus* is far superior to any other. The method is very simple: a leg of either the middle or hind pair is cut off, between the coxa and trochanter if possible, and put on a slide in a drop of water under a very thin covering glass. Care should be taken to have the leg tolerably straight, for if much flexed some of the best parts are obscured. The muscles are here in an almost perfectly normal condition, for their attachments are uninjured, and the water in which the leg is placed (its native element, by the way) can hardly penetrate beyond the joint below the point of division. The only disadvantage is that the specimen is cut off from its nutrient and nervous supplies. A successful experiment affords one of the most striking views in the range of microscopy; the muscular fibres of apparently semi-fluid consistency are in almost constant, though irregular, motion, carrying the smaller branches of the trachiæ to and fro, as seaweed is swung by a wave. These phenomena sometimes continue for an hour and a half, with no other encouragement than an occasional slight tap on the covering glass. The following observations have been made on the trochanter, the femur and the tibia. In the two former it is easier to find places where there is but one layer of fibres, but the tibia is usually preferable, for the shell is more transparent, and there are many fibres attached at different degrees of obliquity to a tendon, so as to illustrate the effect of more or less tension. Moreover, these fibres, owing perhaps to the proximity of a large tracheal dilatation, preserve their irritability much longer than others.

The work of which this paper contains the results, has been done entirely on preparations of this kind of the legs of the *Gyrinus*. The observations were made while the fibres were still capable of contraction. Hartnack's immersion objectives, Nos. 9 and 10 (usually the latter) were employed, with his No. 3 ocular, and the draw-tube drawn out.

As is well known, the muscular fibres of insects are not bound together by interstitial tissue nearly so strongly as those of vertebrates, and each is able to contract freely independently of its neighbors. The states in which muscular fibre is seen may be divided into four chief ones.

The *first state* (Plate II, fig. 1 and fig. 2, *A*) is the essentially normal one in which the fibre is at rest, but extended between points far enough apart, and sufficiently fixed, to oppose a certain resistance to its elasticity and contractility.

The *second state* (fig. 3) is seen when the fibre is free from all strain or resistance; it is that which a fibre in the first state would assume if one of its attachments were divided, or moved much nearer to the other.

The *third state* (fig. 2, *C*), usually owing to contraction of another part, is one in which a part of a fibre is put upon a decided stretch.

The *fourth state* (fig. 2, *B*) comprises all the degrees of active contraction.

In the *first* state the borders of the fibre are straight, and are connected by narrow transverse bands of a black granular structure, which present considerable variation. Usually the minute black granules lie so near together that no other substance is visible between them, but sometimes they are separated into two distinct lines in a transparent ground substance, and again they may be so close together as to give the band an almost homogeneous appearance. On each side of these bands is a glaring white one, usually broader on one side than on the other. As the stage is rotated the brighter band pales, and the dimmer one brightens, while minute changes in the adjustment or illumination produce similar almost indescribable effects.[1] The bright bands are connected by a broad gray stripe, which is midway between two black bands. I have never seen a lighter stripe in the middle of the gray one in muscle inside the body, but can fully confirm the common account of it in fibres pulled from the leg of the fly. To recapitulate; a fibre at rest consists of a series of gray stripes with white borders situated between black granular bands.

The *second* state is best studied on fibres running to the lower part of the tendon that passes from the tibia to the end of the limb, for in many positions of the leg they are completely relaxed, and hang in graceful curves. When, as sometimes happens, the tendon is broken, they are seen to particular advantage. The whole fibre is broader

[1] *Vide* Heppner in Archiv für Mikroskopische Anatomie, Band v, Heft 1.

than in the first state. The black bands are usually somewhat narrowed, and also drawn nearer together. Their granular nature can almost always be made out, but the granules are never seen in two rows. The white and gray stripes are both visible, but are narrower, especially the former, than in the normal condition. The edges of the fibre are scalloped. The ends of each projection come into the borders of the black bands, the greatest bulging being opposite to the middle of the gray.

In the *third*, or stretched condition, the fibre is decidedly narrower, with a peculiarly sharply defined outline. The granular bands are pulled apart into two parallel lines of dots lying in a brilliant clear ground, which is continued into the two white bands. The gray band is lighter, and the bright bands darker than when at rest, so that all parts of the ground substance present nearly, though not quite, the same appearance.[1] The appearances of contracted fibre will be best described in connection with the accompanying phenomena.

On looking at the tibia or femur when the fibres are in active contraction, the attention is constantly distracted by the strangeness of the view, and by the multiplicity and rapidity of the changes in progress. It requires much practice and the closest attention, to fix the eye on a part of a fibre at rest, and to keep it there so as to note the successive changes. If the contraction be very rapid it is probably impossible to do so, but when it is becoming weaker it can be done very fairly; but I must admit that I have not been able to satisfy myself positively on certain points to be presently noticed. This much, however, is certain, namely, that with experience it is easy to follow an individual black band from the state of rest to that of full contraction, which shows that the homogeneous stage (Zwischenstadium), supposed by Merkel to occur in partial contraction. has no existence, and that his theory of an exchange of places between two substances in closed cases is impossible. The general impression given by a wave of contraction is that a part of the fibre dilates, that the black bands become more prominent and, while approaching each other, run with the wave along the fibre. This last appearance is partly true and partly deceptive, for to be drawn together the bands must really move; but the effect is exaggerated by new parts in front of the wave, entering into contraction as those behind it are relaxed. The substance between the black bands is evidently the

[1] In fig. 2, *C*, the difference between the gray and white is too marked.

contractile element. Two or three bands are seen to be drawn quickly nearer together, and the gray substance between them disappears, so that there is an alternation of black and white stripes. This first step of contraction occurs so rapidly that the observer is scarcely aware of it before it is completed, but as the wave runs along the fibre it is more easily observed. The black bands can be seen to approach one another, and sometimes even the granules composing them to get nearer together; in full contraction they are sometimes apparently homogeneous, sometimes granular, but it is important to notice that their edges are rarely sharply defined against the white; they appear irregular and granular. The borders of the fibre are so frequently seen to become scalloped, that I cannot but think it the universal law, though often, owing to the proximity of other fibres, the swellings cannot be seen. At the point of greatest contraction the fibre is much broader than elsewhere, and there is no doubt that the black bands are lengthened; nevertheless they appear longer than they really are, for the bulgings at the ends of the light bands come so near together that they almost touch one another, and their edges being rendered indistinct by optical effects appear, in part, as prolongations of the black bands.

The most puzzling point of all is to decide at just what stage of contraction the gray disappears. This is particularly difficult to observe, because the colors are changing their shades and positions at the same time. It is certain that the gray has disappeared somewhat early in the contraction — say in its first half, and also that it is not the very first change, for it may be seen in very slightly contracted fibres. There does not appear, at least in the detached leg, to be any law regulating the direction of the wave; it seems quite accidental whether it runs toward the tendon or from it. Usually it begins at one end of a fibre, and after a moment's pause runs the whole length, when it either dies out, or, as is more frequently the case, returns, gradually growing weaker, and embracing less of the fibre. When the specimen is fresh and lively, a wave of average size comprises the substance between seven or eight bands, and as long as contraction lasts, rarely less than that of three elements is involved. As the wave runs toward the end of a fibre the part behind it is put more or less upon the stretch, frequently enough so for it to assume the condition already described as the third state. When the contraction is nearly over, it is not rare to see the fibre restored to its normal state by a sudden jerk in the direction opposite

to that pursued by the wave, evidently caused by the elasticity of the stretched portion. The contractile force of the part of fibre in action overcomes the elasticity of the part at rest, but at a certain moment the latter property reasserts itself.

Merkel, as already mentioned, describes a homogeneous appearance as characteristic of a certain stage of contraction. Schäfer, on the other hand, thinks it occurs during perfect rest. For my part I have never seen it at all. In beetles, however, that have suffered from confinement, it is not very rare to find the markings very indistinct, and in some cases many stray granules are found in the fibre, particularly near the surface. I have often noticed the latter appearance after the muscle had become exhausted by electricity. The long muscle corpuscles, well described and represented by Klein,[1] are often seen very near the surface of the fibre. In the living and healthy muscle a longitudinal striation is almost never seen, though it appears in unhealthy fibres. It is superficial, and probably exists solely in the sarcolemma.

The polariscope has been much used, in order to decide on the differences of the nature of certain parts, but the results of different observers are not in harmony, and it may well be questioned whether results obtained by its use on fibres hardened by reagents, are of any particular value. In the case of the entire leg, it proved unavailable for the presence of two layers of shell, enclosing often more than one layer of muscle, rendered the few results which I obtained quite untrustworthy. It has been stated that the staining qualities of hæmatoxylin make it a substitute for polarized light; accordingly I repeatedly put a living beetle into a pretty strong solution; but though I once left one in for twenty-four hours, during the greater part of which time life was extinct, the tissues showed that none of the coloring matter had passed the skin, so that I was obliged unwillingly to give up this class of experiments.

By the kindness of Professor Henry P. Bowditch, I was enabled to perform in his laboratory a series of electrical experiments with both the constant and the interrupted current. The effect of a single shock, or of the use for a short time (say a minute) of a weak interrupted current, was to produce lively, though irregular action; the waves ran in both directions simultaneously. If a strong interrupted current were used, or a weak one were long continued, the muscle became tetanized; the waves of contraction ceased, and

[1] Handbook for the Physiological Laboratory.

whole fibres assumed the appearances of the extremest contraction throughout; nothing could be seen but a succession of very narrow black and white lines. The experiments with the constant current promised to be of great interest, but as they were very difficult, and threatened to lead me far beyond my original plan, I soon decided to leave them for abler hands.

Let us now glance at the difference of the results obtained by this method, and by examining fibres taken from the legs of the large water beetles, Hydrophilus and Dytiscus. For the appearances of those of the Hydrophilus, I have used Heppner's plates (*loc. cit.*), and for those of the Dytiscus, original observations on fibres from the leg without any reagent. The muscles of the two are precisely similar. By comparison with those of the little Gyrinus, *in situ*, it appeared that the fibres of the larger beetles were much broader, but that the stripes were in proportion much nearer together. To see if this did not depend on the abnormal condition of the larger fibres, I endeavored to obtain fibres from the Gyrinus. There was little difficulty in doing this if a leg, or a part of the abdomen, were broken to pieces in a drop of fluid, but unfortunately it was almost impossible to separate the muscles from the shell without such addition, and when a minute piece was fortunately isolated, it, as a rule, immediately became dry and useless. Fig. 4, Pl. II., represents a fibre teased out in glycerine: it shows that the black stripes are strongly drawn together, that their granular structure is indistinct, and that the gray bands are wanting. It is more or less obscured by the longitudinal folds of the sarcolemma which give it a somewhat fibrillated appearance. The particular fibre chosen is not an extreme case; on the contrary, most fibres were much more obscure, and those in water more contracted than those in glycerine. In the few specimens of any value to which no fluid had been added, most of the fibres were less normal than the one drawn, and I can remember but two individual fibres that were decidedly more so. There can be little doubt that if it were possible to examine the fibres of the larger water beetles, *in situ*, that they would present quite different proportions from those usually ascribed to them.

The following are briefly the conclusions which the preceding observations appear to warrant. The fibre consists of a sheath, the sarcolemma, and of a ground substance, in which elements which may provisionally be called granules, are imbedded in transverse double rows. There is no reason to suppose that the difference be-

tween the white and the gray has any other than an optical cause, namely: that the part of the ground substance nearest the black bands receives not only the rays of light that would naturally strike it, but others reflected or refracted, or both, from the black bands, and which do not strike the middle of the space between the latter. (Heppner.Schäfer.) If this be admitted, it is merely a corollary that, in contraction, the gray should disappear; as is the case. No appearances have been seen that are suggestive of the handles of Schäfer's dumbbell-like rods, which, indeed (judging from the abstract of his paper), he has assumed rather than demonstrated. As has been already stated, nothing like fibrillar structure is to be seen in the living and healthy fibre.

The sarcolemma is firmly attached to each edge of the ends of the black bands, and the granules must, in some way, be prevented from separating laterally, so as to give the support for the folds, into which the muscle contracts. The ground substance is the contractile element; it is also highly elastic. When the fibre is stretched all parts become narrower, and when contracted, broader; but in the latter case the change is chiefly in the ground substance.

EXPLANATION OF PLATE 2.

The drawings are all from fibres of the *Gyrinus*, as seen with objective 10 immersion, and No. 3 eyepiece (Hartnack), and are slightly reduced.

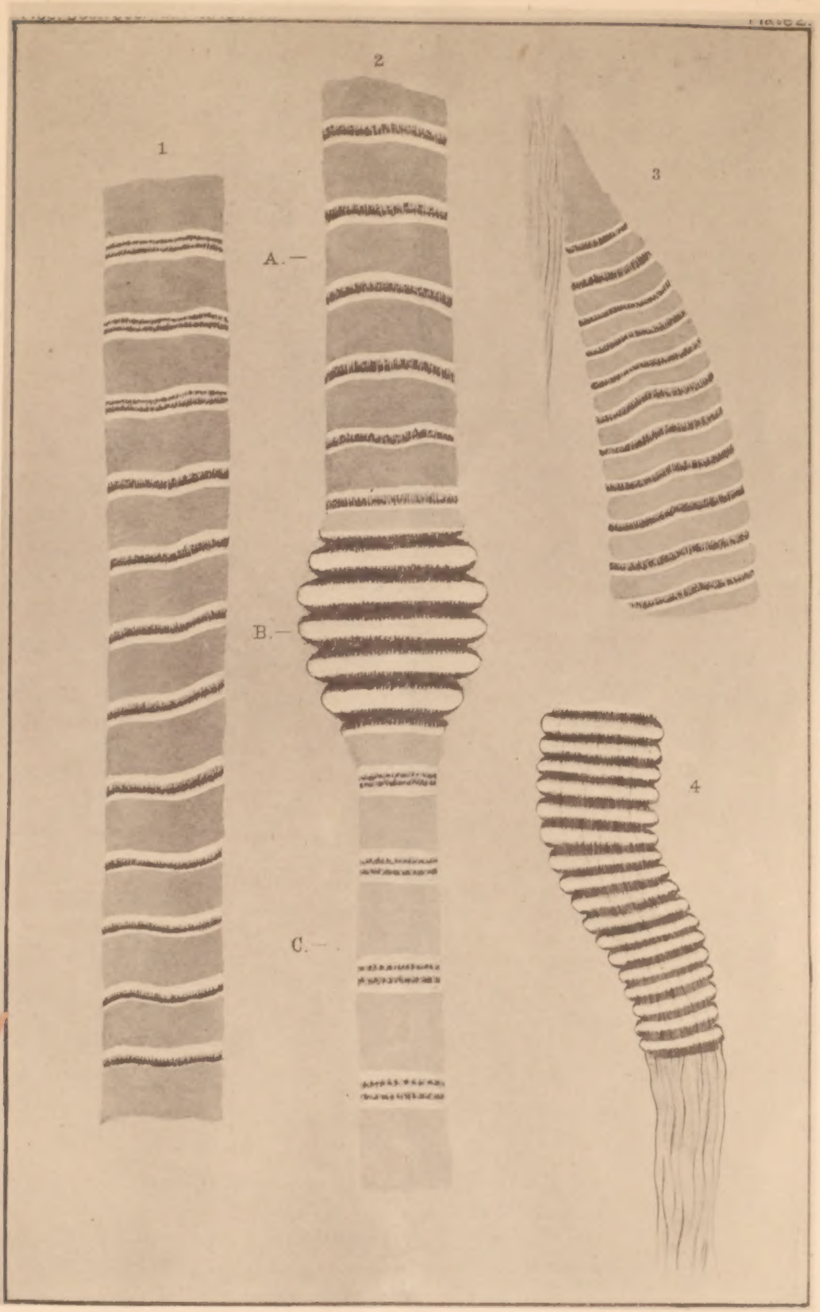
Fig. 1. Muscular fibre at rest under normal conditions, showing the various appearances of the granular and bright bands.

Fig. 2. A fibre at rest at *A*, contracted at *B*, and stretched at *C*.

Fig. 3. A fibre in passive contraction (second state) attached to a tendon.

Fig. 4. A fibre teased out in glycerine.

The drawings are more or less diagramatic, owing to the great difficulties which the object presents. This is particularly the case at *B*, in fig. 2, and can easily be accounted for when it is remembered that the wave of contraction is never stationary for a second. The gray at *C*, in fig. 2, is too dark.



Dr. H. P. Quincy, Del. Heliotype.

DWIGHT, STRUCTURE OF MUSCULAR FIBRE.